



Shared body representations and the "Whose" system

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Abstract: Mirroring has been almost exclusively analysed in motor terms with no reference to the body that carries the action. According to the standard view, one activates motor representations upon seeing other people moving. However, one does not only see movements, one also sees another individual's body. The following questions then arise. To what extent does one recruit body representations in social context? And does it imply that body representations are shared between self and others? This latter question is all the more legitimate since recent evidence indicates the existence of shared cortical networks for bodily sensations, including pain (e.g., Singer et al., 2004) and touch (e.g., Keysers et al., 2004; Blakemore et al., 2005). But if body representations are shared, then it seems that their activation cannot suffice to discriminate between one's body and other people's bodies. Does one then need a "Whose" system to recognize one's body as one's own, in the same way that Jeannerod argued that one needs a "Who" system to recognize one's actions as one's own?

April 11th, 2013

Dear editor,

Please find attached my manuscript “Shared body representations and the “Whose” system” for submission to Neuropsychologia.

Yours sincerely,

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Shared body representations and the “Whose” system

Frédérique de Vignemont

Highlights

Mirroring has been almost exclusively analysed in motor terms with no reference to the body that carries the action. According to the standard view, one activates motor representations upon seeing other people moving. Furthermore, most people have drawn the implications of those shared action representations for 3rd person mindreading (do they allow direct understanding of other people’s intentions?). By contrast, this paper focuses on the existence of shared body representations rather than on shared action representations and on their implications for self-awareness, and in particular on the sense of bodily ownership (how do I recognize this body as my own?).

To what extent does one recruit body representations in social context? And does it imply that body representations are shared between self and others? This latter question is all the more legitimate since recent evidence indicates the existence of shared cortical networks for bodily sensations, including pain (e.g., Singer et al., 2004) and touch (e.g., Keysers et al., 2004; Blakemore et al., 2005). But if body representations are shared, then it seems that their activation cannot suffice to discriminate between one’s body and other people’s bodies. Do we then need a “Whose” system to recognize our body as our own, in the same way that Jeannerod argued that we need a “Who” system to recognize our actions as our own?

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Mirroring has been almost exclusively analysed in motor terms with no reference to the body that carries the action. According to the standard view, one activates motor representations upon seeing other people moving. However, one does not only see movements, one also sees another individual’s body. The following questions then arise. To what extent does one recruit body representations in social context? And does it imply that body representations are shared between self and others? This latter question is all the more legitimate since recent evidence indicates the existence of shared cortical networks for bodily sensations, including pain (e.g., Singer et al., 2004) and touch (e.g., Keysers et al., 2004; Blakemore et al., 2005). But if body representations are shared, then it seems that their activation cannot suffice to discriminate between one’s body and other people’s bodies. Does one then need a “Whose” system to recognize one’s body as one’s own, in the same way that Jeannerod argued that one needs a “Who” system to recognize one’s actions as one’s own?

Keywords: self, bodily ownership, agency, naked intention, mirroring, imitation, interpersonal body representation, peripersonal space, mirror-tactile synaesthesia, vicarious touch, empathy, pain, embodiment

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1. Introduction

A recent trend in the neuroscientific and philosophical literature suggests that we have representations that are shared between self and others (Gallese, 2001; Goldman, 2006). It all started in 1992 when researchers in Parma found that the same neurons fired both when a monkey was grasping a peanut and when it was watching the experimenter grasping it (di Pellegrino et al., 1992; Rizzolatti et al., 1995; Grezes & Decety, 2001). More generally, the motor system is activated not only when an agent executes a goal-directed action, but also when an observer perceives the same action performed by another agent. What makes action mirroring special is that it goes beyond mere conceptual sharing. In Jeannerod (1994)'s terms, one does not share only semantic knowledge about the action; one shares the agent's pragmatic perspective. As such, action mirroring allows the observer to internalize another individual's actions as if she were the agent by a kind of motor simulation.

Most people have drawn the implications of those shared action representations for 3rd person mindreading (do they allow direct understanding of other people's intentions?). By contrast, Marc Jeannerod focuses his interest on their implications for self-awareness and more specifically, for the sense of agency (how do I recognize my actions as my own?). With Elisabeth Pacherie, he argues that shared motor representations consist in what they call naked intentions, that is, intentions that are neutral relative to the agent (Jeannerod and Pacherie, 2004). The naked content can take two forms: either impersonal of the type <action, goal> or personal of the type <x, action, goal>, with x as the parameter of the agent still to be determined (de Vignemont, 2004; Jeannerod and Pacherie, 2004). In any case, the activation of shared motor representations cannot suffice to differentiate whether it is the agent moving or another person moving. Further processes based on extra information are

needed: “Given the existence of shared representations, something more than the sole awareness of a naked intention is needed to determine its author.” (Jeannerod and Pacherie, 2004, p. 140). The lack of differentiation between self and others seems indeed to indicate that one needs a specific mechanism to take apart one’s actions and other people’s actions. Georgieff and Jeannerod (1998) call this mechanism the “Who” system.

Jeannerod analyses mirroring exclusively in motor terms, with no reference to the body that carries the action. However, it seems that in some situations, we need to establish a correspondence between the representation of our body and the representation of other people’s bodies. How do we achieve such correspondence? Are there shared body representations? These questions are all the more legitimate since recent evidence indicates the existence of shared cortical networks for bodily sensations. Brain activity partially overlaps when one experiences touch or pain and when one observes another individual receiving a tactile or a painful stimulus (e.g., Singer et al., 2004; Keysers et al., 2004). Strikingly, people with mirror-tactile synaesthesia even consciously feel tactile sensations on their face upon perceiving another person touched on the face (Blakemore et al., 2005). Like for action, shared cortical networks for bodily sensations have been systematically considered from the perspective of the understanding of other people, and especially in relation to empathy (Goldman, 2011; Banissy and Ward, 2007; Keysers et al., 2010; Ebish et al., 2009, Wood et al., 2010). But what consequences do they have for the sense of bodily ownership? All together, these findings may be taken as evidence of shared body representations. But if body representations are shared, then it seems that their activation cannot suffice to discriminate between one’s body and other people’s bodies. Should we then extend Jeannerod’s conclusion to the sense of bodily

ownership? In other words, do we need a “Whose” system to recognize our body as our own?

2. An embodied approach to the correspondence problem

A classic problem in the imitation literature is known as the intersubjective correspondence problem: how does one map another person’s movements to one’s own movements (Goldenberg, 1995; Heyes, 2001)? The classic way to approach the correspondence problem has been in sensorimotor terms: how does one map visual information to motor command (e.g., Brass and Heyes, 2005)? Alternatively, one can consider that the main challenge is a problem of intermodal correspondence: how does one map visual information to somatosensory information (e.g., Meltzoff and Moore, 1995)? This latter problem can be found not only in imitation (and especially in the case of opaque movements like tongue protrusion for which one has no visual feedback), but also in vicarious bodily sensations experienced when observing other people receiving tactile (or painful) stimulation. However, the question that interests us here is whether there is a further approach to the correspondence problem. In other words, is there a bodily correspondence problem? In imitation, one maps the movement of another body onto one’s body, and in mirror-tactile synaesthesia, one maps the location of touch on another body to one’s own body. For all that, is intersubjective correspondence mediated by bodily correspondence? Shared motor, affective and somatosensory representations have recently been taken as evidence in favour of embodied social cognition (Gallese, 2007; Gallagher, 2005). However, the sense in which those states are embodied remains often obscure. We shall see now that they are two distinct types of shared representations, and only one of them involves body representations.

2.1 Disembodied shared representations

According to a narrow interpretation of the notion of embodiment, shared representations qualify as embodied in virtue of their bodily content (Goldman and Vignemont, 2009). They carry information about the body, and in particular about its spatial properties. In this sense, embodied representations are representations of the body. But there is another interpretation of the notion of embodiment, according to which shared representations qualify as embodied in virtue of their specific bodily format (Goldman and de Vignemont, 2009; Gallese and Sinigaglia, 2011). Bodily format is a class of representational code, which includes somatosensory, interoceptive, affective, and motor codes. It is then one thing to be endowed with a bodily format and it is another thing to have a bodily spatial content. For example, the visual representation of one's hand has a spatial bodily content, but it is not encoded in a bodily format. Conversely, affective states are endowed with a bodily format (because they are associated to - or caused by - certain physiological bodily states), but they do not have a spatial bodily content.

Let us now apply this distinction between content and format to social cognition. With Alvin Goldman, we argued that shared representations – motor, somatosensory and affective – are endowed with a bodily format. In this sense, they are embodied. For all that they do not necessarily represent the properties of the body, and in particular its spatial properties. In this narrower sense, they are not embodied. In other words, the existence of shared representations in bodily format does not necessarily imply the existence of shared body representations. Here I will focus exclusively on the notion of bodily content. The question then is whether action mirroring, vicarious pain and vicarious touch are embodied or disembodied in the narrow sense.

Let us consider first the case of action mirroring. It is useful here to draw the parallel with the distinction between imitation and emulation. Emulation involves the copy of the goal of a perceived action. For instance, upon seeing someone taking an umbrella, one takes an umbrella as well, but the bodily movement can be completely different. In contrast, in imitation not only is the goal copied, but also the bodily movements used to reach the goal. For instance, upon seeing someone taking an umbrella by lifting it with the foot, one performs the same movement instead of simply grasping it with the hand. The difference between imitation and emulation is thus a matter of motor hierarchy: at what level the visually perceived action is analysed and copied. The low level is strongly embodied (imitation), whereas the more abstract levels are weakly embodied (emulation). The question then is at what level action mirroring occurs. To what extent are bodily parameters represented in mirror systems? Does one use body representations to covertly replicate actions that one perceives?

A series of brain imaging studies show that mirroring is closer to emulation than imitation insofar as it encodes the motor goal instead of the specific bodily movement to achieve the goal (Csibra, 2007). On the one hand, the same bodily movement performed for two distinct intentions (grasping a mug for drinking or for cleaning for instance, cf. Iacoboni et al., 2005) activates two distinct brain areas. On the other hand, different bodily movements performed for the same intention (grasping with the mouth and grasping with the hand, cf. Gallese et al., 1996; grasping food with one's hand and with a stick, cf. Ferrari et al., 2005) activate the same brain area. Interestingly, Csibra (2007) notes that the majority of mirror neurons are only broadly congruent. What is shared is not the representation of the specific limb to move, but rather some motor representation higher in the motor hierarchy. Intersubjective

correspondence is then achieved exclusively in motor terms, and not in bodily terms. These findings show how weakly embodied (in the content sense, not in the format sense) the mirror systems can be.

The question of bodily correspondence may then seem more legitimate in the case of vicarious bodily sensations than in the case of action mirroring. At first sight, one may expect the involvement of body representation more systematic, or even necessary, in vicarious pain and in vicarious touch insofar they are vicarious versions of bodily sensations. Yet, this is not the case, as we shall see now.

Let us consider the case of pain first. The pain matrix includes two functionally specialized networks. The sensory-discriminative component involves the experience of the intensity of pain and its bodily location. It recruits primary and secondary somatosensory areas (SI and SII) as well as the posterior insula. Since SI has a somatotopic organization, different regions of SI are activated according to whether one experiences standard pain in one's hand, in one's foot, or in one's mouth. In addition, the sensory-discriminative component has a motor counterpart: its activity underlies specific automatic localized motor responses whose function is to avoid (or decrease) the pain. For instance, the muscles adjacent to the location of the painful stimulus freeze, so to speak. The affective component involves the experience of the unpleasantness of the painful experience. It recruits the anterior insula, the anterior cingulate cortex, the thalamus, and the brain stem. It lacks somatotopic organization.

Now if one experiences vicarious pain, then what happens? Are both components active? More particularly, is vicarious pain localized in a part of one's body that matches the body part that is seen injured? Interestingly, when participants observe cues indicating that another individual is receiving a painful stimulus, most brain imaging studies report a selective activation of the affective component only, with no

associated activation of SI (e.g., Singer et al., 2004). For instance, the same brain activation was found whether the hand or the foot was injured (Jackson et al., 2005). Vicarious affective pain is thus indifferent to the bodily location of pain. This is why one can vicariously experience pain upon either perceiving another's facial expression, which does not reveal the bodily location of the other's pain (Botvinick et al., 2005) or imagining another's non-located painful experience (Jackson et al., 2006). One may conceive vicarious affective pain as a vicarious version of a non-localized bodily feeling of the type "It hurts" (de Vignemont and Jacob, 2012). In this sense, it is disembodied.

One may expect vicarious tactile sensations to be more strongly embodied, since they are generally devoid of affectivity. Yet, this is far from being so. Touch is also characterized by its dual nature, although of a different kind from pain. Touch can be active (touchant) or passive (touché), or both at the same time in self-touch. One can then distinguish between vicarious touchant experience and vicarious touché experience, although they are confounded in most experiments. Several brain imaging studies found activity only in SII, and not in SI, when participants observed another person being touched (Keysers et al., 2004; Ebisch et al., 2008). Interestingly, SII was activated even when participants watched an object being touched, rolls of paper for instance. It thus seems that most of the time vicarious touch takes into account primarily the body part that is touching (vicarious touchant experience): "What is being touched does not matter as long as touch occurs" (Keysers et al., 2004, p. 339). According to Keyser and coll. (2010), vicarious touch corresponds to the mirroring of tactile consequences of action.

To conclude, there is evidence of shared action, shared touch and shared pain, but so far there is no evidence of shared body representations. The intersubjective

correspondence problem is not necessarily encoded in bodily terms. One can map the other onto oneself while bracketing the spatial properties of the body. Shared representations are then disembodied insofar as they do not have a bodily spatial content. Yet, as we shall see now, it can be useful, or even necessary in some situations, to analyse other people's movements and sensations in terms of the body parts that move and that are stimulated.

2.2 Embodied shared representations in imitation

“Body part coding reduces the visual appearance of the demonstrated gestures to simple spatial relationships between a limited set of discrete body parts. Body part coding facilitates imitation because it produces equivalence between demonstration and imitation that is independent of the different modalities and perspectives of perceiving one's own and other persons' bodies, and because it reduces the load on working memory in which the shape of the gesture must be held until motor execution is completed.” (Goldenberg, 2009, p. 1455)

Goldenberg (2009) defends an embodied approach to imitation, according to which one uses knowledge about the body to decode the other's movement and copy it. The special role of body representation in imitation is especially salient for some specific types of actions. This is the case for instance when one imitates meaningless gestures. Upon seeing a military salute, one can recognize it as such and use a stored motor schema of the salute to replicate it. But when one sees a person putting her thumb above her eyebrow, the only solution is to encode the movement in terms of the body parts that are seen and their spatial relations. Hence, it is classically assumed that

there are two routes for imitation: one that involves the recognition of the seen action and the other that does not, and only the latter uses ‘body part coding’ (for review, see Rumiati et al., 2009). Deficits in imitation are then sometimes explained in terms of deficits of body representation. This is the case for instance in patients with ideomotor apraxia who are most affected in the imitation of meaningless gestures (Goldenberg, 1995; Buxbaum et al., 2000; Schwoebel & Coslett, 2005).

Imitation is often considered as the key mechanism for acquisition of new skills. But the use of imitation is not restricted to explicit learning context. Rather, we have a permanent tendency to automatically imitate other people’s movements, which we need to inhibit (Brass et al., 2001). This can be shown if subjects simultaneously perform a movement. For example, participants are faster in moving their index finger when observing an index finger movement than a middle finger movement. Motor facilitation effect is driven by the bodily congruency between the effectors and cannot be reduced to a mere spatial congruency effect. For instance, Brass and coll. (2001) asked participants to observe an index finger tapping and lifting, but the image was inverted (upward motion for tapping and downward motion for lifting). Yet, participants were faster in tapping when observing tapping in spite of the fact that tapping responses (downward motion) were spatially incompatible with tapping stimuli (upward motion) and were spatially compatible with lifting stimuli (downward motion). This study is only one among many other experiments that indicate that how parts of the body are located and move relative to one another is mirrored when observing other people’s actions (e.g. Gillmeister et al., 2008). Interestingly, it was found that the mere observation of coloured patches on another person’s static body parts (head, hand or foot) sufficed to prime action with the same body parts (Bach et al., 2007). The authors concluded in favour of a “body schema that represents

locations on the observer's body and on the bodies of others in a common format" (p. 515). Hence, in some cases, what is shared is not only the representation of the goal or the movement, but the representation of the effector itself that performs the movement. This is confirmed at the neural level. For example, observation of hand, foot and mouth actions selectively activates distinct regions of human ventral premotor and parietal cortex (Buccino et al., 2001). Importantly, Wheaton et al. (2004) showed this somatotopic pattern of activation even when movements were held constant across effectors (opening and closing movements of a hand and a mouth, respectively). Hence, correspondence between self and others can be encoded in bodily terms in some situations.

There are several versions of the bodily approach to imitation. For example, Goldenberg (1995) argues that imitation recruits abstract conceptual knowledge of the human body. By contrast, Chaminade and coll. (2005) as well as Buxbaum and coll. (2000) consider the primitive body schema as the most likely candidate in virtue of its sensorimotor content. Finally, the body image is sometimes also mentioned in virtue of its visuo-spatial content (Gallagher and Meltzoff, 1996). Given the confusion around these various notions (de Vignemont, 2010), I shall leave them aside and instead specify what bodily information needs to be encoded in imitation. A first point is that it must be quite rough-grained. There are many differences between bodies. The body whose movements I copy is never identical to my body: not only is our posture rarely the same, but our gender can also be different, as well as the size of our limbs, the strength of our muscles, the flexibility of our joints, and so forth. Yet this does not prevent intersubjective correspondence. Typically a child can imitate an adult. The brain must thus abstract from major bodily differences. It then seems that what remains in common between all bodies is the configuration of the various body

parts, i.e. the fact that we have two hands and two feet and they are respectively located at the end of our arms and legs. More precisely, what needs to be represented is the functional arrangement of bodily effectors. It was indeed found that the movements that are seen are perceived in terms of functional units of effectors that move together. Functional body parts consist in parts of the body that are regrouped by their role in action. Fingers and hands can constitute grasping units for instance. The foot and the leg can constitute kicking units or walking units. The fact that it is visually shaped like a hand or like a foot and a leg does not matter. For example, observing hand, foot or mouth actions selectively activate brain areas for hand, foot, and mouth even if the movement is performed by non-conspecifics such as monkeys or dogs (Buccino et al., 2004), or robots (Gazzola et al., 2007a; Press et al., 2005). What matters to mirroring is mouth-action, not whether the mouth that is moving is yours or your dog's. The visual appearance and exact shape of the perceived body part are of little importance. What matters is the type of movements it can afford. This is well illustrated by the following finding in aplasic individuals who were born without hands and who perform with their feet and their mouth actions normally performed with hands. It was found that they activated regions of the mirror system recruited in mouth and foot movement execution when observing hand movements (Gazzola et al., 2007b). In mirroring, one matches functional bodily units dedicated to specific types of movements (grasping for instance), no matter whether those functional bodily units are instantiated by a hand or a mouth. Arguably, this level of segmentation of the body into parts is the most relevant for action in general, and for imitation and mirroring in particular. For most gestures one can dispense with more detailed bodily specification. All that needs to be represented is the dynamic position of functionally defined body parts with respect to one another (Buxbaum et al., 2000).

2.3 Embodied shared representation in vicarious sensations

Intersubjective correspondence recruits body representations not only in imitation, but also for some vicarious bodily sensations. Vicarious pain can be of two distinct kinds. It includes not only vicarious affective pain, which is disembodied, but also vicarious sensory pain, which is embodied (de Vignemont and Jacob, 2012). For instance, it was found activation of the somatopically organized SI upon seeing the back of another's hand being deeply penetrated by a needle (Bufalari et al., 2007). Motor responses to vicarious sensory pain are even muscle-specific, similar to those found when one is injured: when one sees another's hand being hurt, one automatically freezes one's own hand, as if one's own hand were injured (Avenanti et al., 2005; 2009). These experimental results strongly suggest that in experiencing vicarious sensory pain, one responds to the perception of another's bodily part subjected to painful stimulation by expecting specific sensorimotor consequences of pain at the same location on one's own body.

Likewise individuals with mirror-touch synaesthesia consciously feel tactile sensations on their own body when they see another person's being touched (Blakemore et al., 2005; Banissy and Ward, 2007). Upon seeing another being touched on the left cheek for example, they experience a sensation of touch on their own cheek. If at the same time they are touched on the right cheek, they either report feeling touch on both sides or they make mistakes (they report feeling touch on the left). This is not a mere attentional effect. They do not make mistakes if they see a visual flash on the left of the face rather than receive a tactile stimulus (Banissy and Ward, 2007). When compared to normal subjects, it was found a more intense activity of the somatosensory cortex when subjects with mirror-tactile synaesthesia saw

people being touched (Blakemore et al., 2005). In addition to individuals with mirror-tactile synaesthesia, it was found that some patients with phantom limbs reported feeling tactile sensations on their phantom hand when observing another person's hand being touched (Ramachandran and Brang, 2009).

The interpersonal dimension of body representations in the sensory domain is confirmed by results both in the multisensory literature and in the neuropsychological literature. It is well known that viewing the body part that is touched (without viewing the touching object) enhances tactile acuity so that one's judgements about tactile sensations are both faster (Tipper et al., 1998) and more accurate (Kennett et al., 2001). Importantly, the effect of visual enhancement of touch is as effective when seeing one's own body part as when seeing another person's body part (Haggard, 2006). Likewise, Thomas and coll. (2006) found that participants were faster in detecting touch when they saw before a non-predictive visual cue on another person's body at the corresponding location. The authors concluded: "We believe that our results provide the first behavioural evidence in normal subjects for interpersonal body representation based on a somatotopic spatial map, at the purely sensory level." (Thomas et al., 2006, p. 328). Findings in neuropsychology also indicate the existence of a similar body representation for perception that is 'interpersonal'. Most – but not all – patients with autotopagnosia fail to locate body parts not only on their own body, but also on other people's bodies, on mannequins and on drawings of a human body.

Hence, one exploits body representations in order to map the location of the tactile or painful stimulation of another's body onto one's own body. One can speculate that like in action, bodily coding in vicarious sensations must go beyond the differences between bodies and carry information only about the configuration of the body. But the spatial organization of the body is not similarly represented in imitation and in

1 vicarious bodily sensations. Whereas the representation of the body that is used in
 2 imitation represents functionally defined body parts, the representation of the body
 3 that is used in vicarious bodily sensations represents anatomically defined body part.
 4
 5 One may for instance note that the disruption of the representation of the
 6 configuration of the body in patients with autotopagnosia does not affect their actions.
 7
 8 Unfortunately, there is little evidence on the spatial organization of body
 9 representation in the case of vicarious bodily sensations. The distinction between a
 10 functional and an anatomical representation of the body, however, is in line with a
 11 classic distinction between two types of body representation, one oriented towards
 12 action and the other towards body perception (Dijkerman & de Haan, 2007;
 13 Gallagher, 2005; Head & Holmes, 1911; Paillard, 1980; de Vignemont, 2010). The
 14 two types of body representation follow distinct principles of spatial organization (de
 15 Vignemont et al., 2005; de Vignemont et al., 2009; Tsakiris et al., 2006; Hach et al.,
 16 2011). In particular, action requires a more unified map of the body than perception:
 17 when I move my forearm, my hand and fingers follow. By contrast, if someone
 18 touches my forearm, this usually does not tell me anything about the sensation in my
 19 hand and fingers. On the basis of the results described above, it seems that both types
 20 of body representation can be recruited in social context.

2.3 Embodied shared representations of peripersonal space

1 There is a last series of evidence that argue in favour of shared body
 2 representations. We know that the space immediately surrounding one's body, namely
 3 peripersonal space, is processed differently than extrapersonal space (for review,
 4 Brozzoli et al., 2012). A large number of studies with monkeys have now found
 5 bimodal neurons in several brain structures (putamen, parietal and premotor area),

which are activated both by touch and by vision (or audition). Interestingly, they are
 activated even when the visual stimulus is not on the body part itself, but up to 30-
 50cm off the body part (e.g., Cooke and Graziano, 2003). Moreover, the visual (or
 auditory) activity follows the position of the tactile receptive field associated to a
 specific part of the body when the part is moved. It is thus body-centered. Several
 studies support the existence of a similar multimodal representation of peripersonal
 space in humans, which results in the interaction between visual (or auditory)
 stimulus near the body and tactile processing. The best known evidence in favour of
 such multimodal interaction is the cross-modal congruency effect. Participants are
 asked to report when they feel a vibrotactile stimulation and to judge its location. It
 was shown that neutral visual stimuli interfere with tactile detection and tactile
 localization, if the location of the visual stimuli is incongruent with the location of the
 tactile stimuli (Spence et al., 2004). This effect works only if the visual stimuli are
 close to a part of the body. For such interference to happen, both visual and tactile
 experiences must share a common spatial frame of reference. It is not the visual frame
 because the interference is not sensitive to bodily posture. If the flash of light is close
 to your left hand and the touch is applied to your right hand, your performance
 decreases even if your hands are crossed. Hence, even if the flash is visually located
 close to the hand that is touched, they are not perceived as being congruent. As
 Graziano and Gross (1993, p. 107) described it, the peripersonal space is like “a
 gelatinous medium surrounding the body that deforms whenever the head rotates or
 the limbs move”.

Objects in peripersonal space are endowed with a special significance for the body.
 They may be perceived as potential threats or obstacles. The function of information
 processing in peripersonal space is not uniquely to avoid snakes, and other life-risking

1 situations. One needs to protect one's body in everyday life as well, as when one walks
 2 through a room without hitting the furniture, one brushes away an insect, one reaches
 3 safely around a prickly object, or one sits at a desk without bruising one's elbows and
 4 arms as one works. Objects in peripersonal space may also be perceived as potential
 5 targets for action. One may question whether there is a single peripersonal space or two,
 6 one defined as margin of safety and the other defined as reaching space, but I shall leave
 7 this question aside and focus instead on the representation of other people's peripersonal
 8 space. A series of evidence indeed indicates that it recruits the same resource as the
 9 representation of one's peripersonal space.

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Ishida and coll. (2010) found in monkey parietal areas that some visuo-tactile neurons fired when a visual stimulus was close both to a part of the monkey's body and to the experimenter's equivalent body part. The effect was body part specific. Likewise in humans, it was found that SI was activated when the experimenter stroked with a paintbrush the region of space close to a hand visually presented from a third-person perspective (Schaefer et al., 2012). Surprisingly, however, the activity was stronger than when the experimenter stroked the peripersonal space of a hand visually presented from a first-person perspective. In addition, it was shown that one represents other people's reaching space in the same way as one represents one's reaching space. For example, it is known that the motor system is activated by the mere vision of a graspable object. Furthermore, it has been shown that the spatial alignment of the object with the effector affects the motor response. For example, if the handle of a mug is aligned with the left hand, one is quicker if using the left hand than the left hand to grasp it. This effect works, however, only if the mug is in the agent's reaching space (Costantini et al., 2010). Now a recent study showed that the effect worked as well if the mug was in a virtual individual's reaching space, although

1 it was not in the participants' own reaching space. There was no effect, on the other
 2 hand, if the mug was close to a cylinder of the same size as the virtual avatar. Neither
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 4 was there any effect if there was a near-transparent panel between the avatar and the
 5 mug (Costantini et al., 2011). Cardellicchio and coll. (2012) further showed that
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 7 motor-evoked potentials were higher when the mug was close either to the
 8 participants or to the avatar. The authors concluded: "Our proposal is that such
 9 sensitivity can be explained by means of an interpersonal bodily space representation
 10 allowing one to map the body of other people in terms of their actual motor
 11 possibilities." (p. 4).
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22 To conclude, there are several ways to solve the intersubjective correspondence
 23 problem. In the domain of mirroring, it can involve representations of the motor goal.
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 25 In the domain of vicarious bodily sensations, it can involve affective representations.
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 27 Those representations qualify as embodied insofar their mental format is concerned.
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 29 But they do not qualify as embodied in a narrower sense: they do not represent bodily
 30 states. Yet, there are cases in which the correspondence problem is solved thanks to
 31 representations of the body. Some cases of imitation as well as some vicarious bodily
 32 sensations respect bodily congruency. In order to do so, they need to exploit a
 33 representation of the body to map other people's bodies to one's own body. The body
 34 is then the common "currency" between self and others. And this is so both in the
 35 motor and in the perceptual domains.
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49 But what consequences does it have for the sense of bodily ownership? Jeannerod
 50 and Pacherie's argument for the sense of agency can be articulated into four steps: (i)
 51 there are representations shared between self and others; (ii) thus, they must be
 52 endowed with a naked content (neutral relative to the agent); (iii) thus, they can lead
 53 to confusion between self and others; (iv) thus, one needs a "Who" system. We shall
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now ask whether this argument can apply to the sense of bodily ownership and whether the evidence reviewed so far raises a challenge for theories of bodily ownership, in the same way that the existence of shared action representations raises a challenge for theories of agency. I will now consider two ways to escape Jeannerod and Pacherie's argument. First, one may object to the very first step: there are no representations shared between self and others, but only a coupling of self-specific and non self-specific representations. Second, one may object to the transition from the second step to the third step: naked content does not necessarily open the door to confusion.

3. A matter of coupling?

Intersubjective correspondence can be encoded in bodily terms. So far I have assumed that it involves shared body representation, that is, a single representation exploited for both one's body and other bodies. There is, however, an alternative model that can account for the evidence reviewed above. Intersubjective correspondence can also be achieved by the automatic association of distinct representations. This latter view has been defended among others by Celia Heyes (2001). According to the Associative Sequence Learning (ASL) model, imitation is based on past experiences of the systematic coupling between the action one performs and its sensory consequences. Typically, when I wave my hand, I see it waving. I can thus learn the sensorimotor association so that when I see another person waving, the sensory input can automatically elicit the associated motor output. Another example can be found in Gallagher and Meltzoff (1993). They argue that imitation depends on the systematic association between the body schema, which is primarily proprioceptive and motor, and the body image, which is primarily visual. One can

also interpret some of the multisensory results along these lines. On the basis of their findings that the vision of non-predictive cues of another person's body could interfere with tactile processing on one's own body, Thomas and coll. (2006) defined shared body representations in terms of "a special, automatic mechanism for associating sensory body events" (p. 327).

These different conceptions do not directly address the question of the specific content of the representations that are associated. In particular, are those representations naked? Are they neutral relative to the owner of the body? Let us consider in more detail the ASL model. The two terms of the association are (i) a motor representation, which consists in the activity of the mirror system at the neural level, and (ii) a visual representation of the movement. The visual representation can represent either one's own movement or another person's movement. In this sense, it can be said to be naked. The seen movement is unattributed. The motor representation, on the other hand, is always used for one's own motor system. It plays a role for one's own actions, and one's own actions only. Hence, one may argue that it is first-personal (although not necessarily reflexively). The association can thus be reformulated as follows: an intention <I raise my finger> associated to a visual representation <a finger raising>. The association was built on the basis of past experiences of seeing my finger raising when I have the intention to raise my finger. But it has generalized to any raising finger. Hence, when I see you raising your finger, this activates my mirror system and I have an automatic tendency to imitate the movement. On this view, the motor representation is activated by another person's actions, but for all that it does not represent intentions other than one's own. Only the visual representation has a naked content, not the motor representation. We can apply the same analysis to mirror-tactile synaesthesia. Then the association is between a

tactile representation <touch on my cheek> and a visual representation <tactile stimuli on a cheek>. Again, only the visual representation has a naked content, even if the tactile representation is activated by another person being touched.

If this is the right interpretation, then it is misleading to talk of ‘shared representation’. The results described in the first section are merely a matter of coupling, rather than sharing. They have no implication for the content of the motor and the somatosensory representations. All they imply is that visual representations have a naked content, but this is hardly surprising. Discriminating one’s body from other bodies is then not an issue. As Gallagher and Meltzoff (1996, p. 225-226) noted, “Thus there is a coupling between self and other, and this coupling does not involve a confused experience”. The body representation associated to the visual representation of other people’s bodies can remain self-specific. One can thus dispense with a “Whose” system. The possibility of bodily correspondence has no consequence for the sense of bodily ownership.

However, one may challenge Gallagher and Meltzoff’s conclusion: coupling can lead to confusion if the coupling is mandatory. If the activation of one representation automatically and systematically induces the activation of the other, and vice-versa, then the coupled representations behave as if they constitute a unique representation.¹ It would be like marriage: after a while, you can never invite one spouse without the other; they have lost their individuality. More than coupling, one should then talk of fusion, which can lead to confusion. And if this is the case, then we are back to our original problem. If the couple is activated both by seeing one’s body and other people’s bodies, then the activation of the couple can no longer suffice to discriminate among bodies.

¹ I would like to thank Wolfgang Prinz for this objection.

The question is thus whether the coupling is mandatory or not. If it is, then it does not make much functional difference with actual sharing. To settle the debate, one must look at the empirical data. However, the evidence is not straightforward. On the one hand, some results indicate that the association can allow for some flexibility and plasticity. For example, it has been shown that automatic imitation is sensitive to sensorimotor learning (Cook et al., 2010). Body part priming in imitation was reduced following the repeated exposure to incongruent sensorimotor associations such as observing a hand action while performing a movement with the foot. On the other hand, other findings indicate a tight coupling, so tight that there are bidirectional relations between the two terms of the association.

Most studies have investigated the effect of the observation of others upon oneself, but a few studies showed that the representation of one's body influences the perception of other people's bodies. For example, when participants observe two photographs that differ only in the position of one limb that alternates, they see an illusory movement of the limb. If the photographs are flashed in rapid succession, they perceive the limb traversing the shortest possible path of visual apparent motion, although it is biologically impossible because of joint constraints. But if the presentation rate slows down, they perceive paths of apparent limb movement that follow natural human limb trajectories (Shiffrar and Freyd, 1990). This result indicates that knowledge of one's joint constraints determines how one perceives other people's bodily movements. This effect is not driven by mere visual familiarity of other people's movements, as shown by a study with two aplasic patients born with no arm (Funk et al., 2005). They shared the same visual familiarity of the movements that are biologically possible, but only one of the patients experienced phantom arms, and thus, had bodily familiarity with joint constraints. Interestingly, it was found that

only this patient showed the same perceptual pattern as normal subjects. Hence, the representation of one's bodily constraints can affect the perception of another individual's bodily movements. Another study showed that healthy participants were more efficient in detecting changes in a model's leg posture than in the model's arm posture if they were moving their legs, and conversely that they were more efficient in detecting changes in a model's arm posture if they were moving their arms (Reed and Farah 1995). Hence, not only does the perception of another person's movement affect one's own movements (other-to-self), but one's own movements can also facilitate the perception of another's body (self-to-other). These results do not offer a definite reply about the strength of the association, if association there is. Still they argue in favour of a strong coupling, or even of actual sharing. Let us now consider the implications of the hypothesis that body representations can be shared between self and others.

4. A "Whose" system?

If there are shared body representations, then the same representations are activated both for one's body and for other people's bodies. In order for body representations to fulfil their intersubjective function, they must thus represent what one's body and other bodies have in common, and only that. In Jeannerod and Pacherie's terms, they must have a naked content. Their content is neutral relative to whose body it is. They leave the body unattributed and represent indifferently one's body and other people's bodies. They can be either impersonal representations of the type <body part, bodily property> or personal representations with the owner *x* left unspecified of the type <*x*, body part, bodily property>. Thanks to their naked content they enable the perceiver to imitate another individual's actions and to map her

sensations onto the perceiver's body. What can then be the content of naked body representations? On the basis of his findings on ideomotor apraxia, Goldenberg (1995, p.71) proposes the following characterization: a "general concept of the human body which applies regardless of whether one's own body is concerned or not". But if this is the right way to characterize shared body representations, then they can hardly ground the sense of bodily ownership. It then seems that one cannot dispense with a "Whose" system.

4.1 The Comparator models of ownership

According to Jeannerod and Pacherie (2004, p. 139-140), the existence of shared action representations implies that they cannot ground the sense of agency: "If, however, we can be aware of both our intentions and those of others in the same way, namely as unattributed or 'naked' intentions, the problem of self-other discrimination does indeed arise (...) this cortical network provides the basis for the conscious experience of goal-directedness—the primary awareness of intentions—but does not by itself provide us with a conscious experience of self- or other-agency." Likewise one may argue that because of their naked content, shared body representations cannot suffice to distinguish between one's body and other people's bodies. The impossibility lies in the fact that it cannot solve two opposite problems: the correspondence problem in intersubjective situations and the ownership problem. If at some level the representation of one's body is similar to the representation of other people's bodies, then how could it ground the sense of ownership? It seems that the naked body representation would have to play two incompatible roles: grounding self-awareness and grounding other-awareness. It thus follows from the existence of naked

body representations that further processes are needed to discriminate between one's body and other people's bodies. But what is the exact nature of the "Whose" system?

In the recent philosophical and empirical literature, the prominent view is that the sense of agency should be understood as the result of the comparison between the prediction of the sensory consequences of one's actions and their actual consequences. Can one generalize the comparator model to the sense of body ownership? But then what are the different types of information to compare? In the case of the sense of agency, there is efferent information that can be compared to sensory information, but this is not true in the case of the sense of ownership. Arguably, one can feel one's body as one's own although one is not moving. What type of information can help differentiate one's body from other bodies?

The dominant model of the "Whose" system is entirely drawn from the Rubber Hand Illusion (RHI): synchronous stroking of one's own occluded hand and an anatomically congruent visible rubber hand leads to a sense of ownership over the rubber hand. On the basis of the RHI, it has been suggested that intermodal matching plays a key role for ownership (Botvinick and Cohen, 1998, Makin et al., 2008, but also Rochat 1998 for developmental evidence): "It has been proposed that the body is distinguished from other objects as belonging to the self by its participation in specific forms of intermodal perceptual correlation" (Botvinick and Cohen, 1998, p. 756). In support of this view, it was found that the ownership rating in questionnaires was correlated with the activity in brain regions that are classically involved in multisensory processes: "the detection of correlated multisensory signals by these regions [premotor cortex and posterior parietal area] is the mechanism for body ownership." (Ehrsson et al., 2005, p. 10571).

However, the hypothesis of intermodal matching leaves many questions unanswered. As pointed out by Botvinick and Cohen (1998), one still needs to determine the “special ingredient” for ownership. Indeed, the sense of body ownership cannot derive from any kind of intermodal correlation. Imagine that you see and hear two hands clapping. Despite visuo-auditory correlation, you do not feel these hands as your own. You also need the visuo-auditory information to correlate with proprioceptive and tactile information indicating that you, and nobody else, are clapping your hands. In other words, there must be information that is self-specific (e.g. somatosensory information) for intermodal correlation to play a role for ownership. Furthermore, there are some constraints that lay upon the RHI. For instance, visuo-somatosensory correlation fails to elicit an ownership illusion when the rubber hand is replaced by a wooden spoon (Tsakiris and Haggard, 2005). Hence, Tsakiris (2010) argues in favour of a multi-layered “Whose” system that involves three distinct comparators: between the visual form of the viewed object and a pre-existing body model, between the current state of the body and the postural and anatomical features of the body-part that is to be experienced as one’s own, and between the vision of touch and the felt touch and their respective reference frames.

However, although the RHI has been used as the experimental paradigm to investigate the sense of ownership, one can question whether the same type of mechanisms are at stake for the ownership of the rubber hand, which is merely seen, and for the ownership of a biological hand, which can be moved and experienced from the inside independently of any visual feedback. A recent lesion study showed dissociation between patients who failed to experience the RHI and patients who denied ownership of their own hand (Zeller et al., 2011). The authors concluded that the RHI recruits different brain regions than those involved for the sense of ownership

of one's biological body. One can also question whether there are alternative accounts of ownership that do not appeal to a "Whose" system despite the existence of shared body representations. I will now argue that the existence of naked body content does not necessarily lead to confusion between self and others.

4.2 The Janus head hypothesis

The debate here is far broader than about some putative "Whose" system. What is at stake is whether the exploitation of common resources prevents or reduces the modularity of the mind. According to the modular view, the brain is organized in specialized separately modifiable cognitive abilities that use specific, dedicated neural resources. A modularist may for example claim that some are dedicated to the self and others are dedicated to social cognition. However, more and more evidence indicates that brain regions are not recruited by a single task. Rather, they are recycled to support numerous cognitive functions (e.g., Anderson, 2010, Dehaene and Cohen, 2007; Goldman, 2012). In other words, they are originally established for one purpose and reused for a different cognitive purpose. Recycling makes sense from an evolutionary perspective insofar as it is more parsimonious than developing new neural systems. But does it challenge the modular conception of the mind?

The fact that there are modules does not preclude those modules from sharing parts wherever possible (Carruthers, 2006, p. 23): "As a result, what we should predict is that while there will be many modules, those modules should share parts wherever this can be achieved without losing too much processing efficiency". This may work along the "time-sharing model" offered by Jungé and Dennett (2010, p. 278): "(1) At any given time, one high-level process uses the "workings" of multiple lower-level

areas, and (2) numerous high-level processes are hypothesized to alternately access a common pool of specialized lower-level resources”. The point is that modules are not exhausted by the parts that are shared. If the parts that are not shared are disrupted or modified, then it alters only one module and not the other. Likewise, shared body representations do not mean the end of the boundary between self and others. What is shared is the representation of the rough structure of the body, either for action or for perception. But this rough structure needs to be filled in for a full-fleshed spatial representation of one’s body, including information about body metrics for example, which is highly specific and can hardly be shared. Hence, some processing of bodily information constitutes a common resource between self and other people, which can in turn be used for one or the other. But what is shared, and thus naked, is only one component of more complex representations of the body that are not shared. Those more complex body representations may be called “superficial schema” (Head and Holmes, 1911), “body structural description” (Schwoebel and Coslett, 2005) or “long-term body image” (O’Shaughnessy, 1980). All refer to more or less the same notion, that is, the representation of the spatial configuration and the dimension of the body, what I call myself a body blueprint. One peculiarity of the body blueprint is that its spatial organization differs whether it is used to shape bodily experiences or to guide action.

To recap, some components of the body blueprint are shared between self and others, but some components only. This is confirmed by brain imaging studies, which never show perfect identity between activation for the self and activation for others. For instance, vicarious touch can activate SI, but this hardly exhausts the neural basis of the representation of the spatial properties of one’s body, which includes brain areas at a higher level, including the parietal area. There are differences even in visual

representations of the body. For example, it was found that in the extrastriate body area in the visual cortex, different brain regions selectively responded to images of one's own body parts or other people's body parts (Myers and Sowden, 2008). Furthermore, it was found an implicit self-advantage in body visual recognition (Frassinetti et al., 2008, 2012). Participants were asked to match pictures of body parts together. Their performance improved when the pictures displayed their own body parts from an egocentric perspective compared to when they display other people's body parts from the same perspective. Hence, they were better in visually processing their own body than any other bodies.

The fact that self and others are not fully confounded is also confirmed by neuropsychological dissociations. For example, patients with anorexia nervosa were asked to imagine walking through a door-like aperture and then to judge whether or not they would be able to walk at a normal speed without turning sideways (Guardia et al., 2012). Alternatively they were asked to imagine another person of the same size walking through the aperture and to judge whether she could pass. It was found that the patients mistakenly judged that they could not pass in apertures in which they accurately judged other people could pass. One way to interpret the results is that the blueprint of their own body was impaired with no consequence on the representation of other people's bodies. Conversely, patients with heterotopagnosia have selective difficulties in locating another individual's body parts on her body, but no difficulty on their own body. Rather than pointing on another's body, they indicate the location of the named body part on their own body (Felician et al., 2003). Consequently, deficits of the blueprint of one's body do not necessarily lead to intersubjective impairments.

We can then propose the following hypothesis:

Janus head hypothesis: Intersubjective correspondence is achieved by time-sharing processing of bodily information that is common to the blueprint of one's body and the blueprint of other people's bodies.

On this view, neural resources that were originally designed to represent one's bodily states and were later shaped to represent other people's states are Janus-faced. They face inward as representation of one's body and they face outward as representation of other people's bodies. They can thus bridge the gap between one's body and other people's bodies, but without losing the distinction between self and others. At the level of the body blueprint, representations of one's body still differ from representations of other people's bodies. They are not shared, and thus, they cannot lead to confusion. It then seems that one can dispense with a "Whose" system despite the existence of shared body representations. The content is not naked at all levels. The blueprint of one's body is not exhausted by what is shared. It can thus keep its self-specificity, and thus, suffice to ground the sense of body ownership.

Conclusion

Do we need a "Whose" system like we have a "Who" system? Here I have addressed these questions by analysing the implications of intersubjective correspondence for the content of body representations. I have defended a limited embodied approach to the problem, according to which intersubjective correspondence is encoded in bodily terms in some – but not all – situations. There are shared body representations endowed with naked content, both in the motor and in the perceptual domains, but that they do not exhaust the blueprint of the body, that is, the representation of the spatial properties of the body. Some components of the body

blueprints are naked, but others are not. Hence, body blueprints do not leave the body unattributed. They are thus susceptible to ground the sense of body ownership. It thus seems that one can dispense with a WHOSE system despite the existence of shared body representations.

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References

- Anderson, M. (2010). Neural reuse: A fundamental organizational principle of the brain. *Behavioral and Brain Sciences*, 33, 4, 245-313.
- Avenanti A, Buetti D, Galati G, Aglioti SM (2005) Transcranial magnetic stimulation highlights the sensorimotor side of empathy for pain. *Nat Neurosci* 8(7):955–960
- Avenanti, A., Minio-Paluello, I., Sforza, A. and Aglioti, S.. (2009). Freezing or Escaping? Opposite Modulations of Empathic Reactivity to the Pain of Others. *Cortex* 45 (9): 1072–77.
- Bach P, Peatfield NA, Tipper SP. (2007). Focusing on body sites: the role of spatial attention in action perception. *Exp Brain Res*. 178(4):509-17.
- Banissy MJ, Ward J (2007). Mirror-touch synaesthesia is linked with empathy. *Nat Neurosci* 10:815–816

- Blakemore S-J, Bristow D, Bird G, Frith C, Ward J (2005) Somatosensory activations during the observation of touch and a case of vision-touch synaesthesia. *Brain* 128:1571–1583
- Botvinick, M., and Cohen, J. (1998). Rubber hands ‘feel’ touch that eyes see. *Nature*, 391, 756.
- Botvinick, M., Jhab, A., Bylsmaa, L., Fabian, S., Solomon, P. and Prkachin, K. (2005). “Viewing Facial Expressions of Pain Engages Cortical Areas Involved in the Direct Experience of Pain.” *Neuroimage* 251:312–19.
- Brass M, Bekkering H, Prinz W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychol (Amst)*. 106(1-2):3-22.
- Brass, M., & Heyes, C. (2005). Imitation: Is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences*, 9, 489-495.
- Brozzoli, C., Makin, T.R., Cardinali, L., Holmes, N.P., Farnè, A. (2012) Peripersonal Space: A Multisensory Interface for Body–Object Interactions. In MM Murray, MT Wallace (eds). *The Neural Bases of Multisensory Processes*. Boca Raton (FL): CRC Press
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G. and Freund, H.-J. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: An fMRI study. *European Journal of Neuroscience*, 13, 400-404.
- Buccino, G., Lui, F., Canessa, N., Patteri, I., Lagravinese, G., Benuzzi, F., Porro, C. A., & Rizzolatti, G. (2004). Neural circuits involved in the recognition of actions performed by nonconspecifics: An FMRI study. *Journal of Cognitive Neuroscience*, 16(1), 114-126.

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- Bufalari, I., Aprile, T., Avenanti, A., Di Russo, F., Aglioti, S. (2007). Empathy for Pain and Touch in the Human Somatosensory Cortex. *Cerebral Cortex* 17 (11): 2553–61.
- Buxbaum LJ, Giovannetti T, Libon D. (2000). The role of the dynamic body schema in praxis: evidence from primary progressive apraxia. *Brain Cogn.* 44(2):166-91.
- Cardellicchio P, Sinigaglia C, Costantini M. (2012). Grasping affordances with the other's hand: A TMS study. *Soc Cogn Affect Neurosci.*
- Carruthers, P. (2006). The architecture of the mind: Massive modularity and the flexibility of thought. Clarendon Press.
- Chaminade T, Meltzoff AN, Decety J. (2005). An fMRI study of imitation: action representation and body schema. *Neuropsychologia.* 43(1):115-27.
- Costantini M, Ambrosini E, Tieri G, Sinigaglia C, Committeri G (2010) Where does an object trigger an action? An investigation about affordances in space. *Experimental Brain Research* 207: 95.
- Costantini M, Committeri G, Sinigaglia C. (2011). Ready both to your and to my hands: mapping the action space of others. *PLoS One.* 6(4):e17923.
- Cook R, Press C, Dickinson A, Heyes C. (2010). Acquisition of automatic imitation is sensitive to sensorimotor contingency. *J Exp Psychol Hum Percept Perform.* 36(4):840-52
- Cooke, D. F., and Graziano, M. S. A. (2003). Defensive movements evoked by air puff in monkeys. *Journal of Neurophysiology*, 90, 3317–3329.

- Csibra G (2007) Action mirroring and action interpretation: An alternative account. In
Haggard P, Rosetti Y, Kawato M (eds) Sensorimotor foundations of higher
cognition. Attention and performance XXII. Oxford University Press, Oxford
- Dehaene, S. & Cohen, L. (2007) Cultural recycling of cortical maps. *Neuron* 56:384–
98.
- de Vignemont F (2004) The co-consciousness hypothesis. *Phenomenol Cogn Sci*
3:97–114
- de Vignemont, F. (2010) Body schema and body image: pros and cons.
Neuropsychologia, 48(3), 669–80.
- de Vignemont, F., Tsakiris, M., Haggard, P. (2005), Body mereology. In *Human
Body Perception from the Inside Out*, edited by G. Knoblich, I.M. Thornton, M.
Grosjean, M. Shiffrar. New York: Oxford University Press, 147-170.
- de Vignemont, F., Majid, A., Jolla, C., and Haggard, P. (2009). Segmenting the body
into parts, evidence from biases in tactile perception. *Quarterly Journal of
Experimental Psychology*, 3, 1–13.
- de Vignemont, F. and Jacob, P. (2012), What it's like to feel another's pain.
Philosophy of Science, 79, 2, 295-316.
- Dijkerman, H. C., and de Haan, E. H. (2007). Somatosensory processes subserving
perception and action. *The Behavioral and Brain Sciences*, 30, 189–201.
- Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992).
Understanding motor events: a neurophysiological study. *Experimental Brain
Research*, 91, 176-180.

- Ebisch SJ, Perrucci MG, Ferretti A, Del Gratta C, Romani GL, Gallese V. (2008). The sense of touch: embodied simulation in a visuotactile mirroring mechanism for observed animate or inanimate touch. *J Cogn Neurosci*. 20(9):1611-23.
- Ehrsson HH, Holmes NP, Passingham RE. (2005). Touching a rubber hand: feeling of body ownership is associated with activity in multisensory brain areas. *J Neurosci*. 25(45):10564-73.
- Felician O, Ceccaldi M, Didic M, Thinus-Blanc C, Poncet M. (2003). Pointing to body parts: a double dissociation study. *Neuropsychologia*. 41(10):1307-16.
- Ferrari PF, Rozzi S, Fogassi L (2005) Mirror neurons responding to observation of actions made with tools in monkey ventral premotor cortex. *J Cogn Neurosci* 17:212–226
- Frassinetti F, Maini M, Romualdi S, Galante E, Avanzi S. (2008). Is it mine? Hemispheric asymmetries in corporeal self-recognition. *J Cogn Neurosci*. 20(8):1507-16.
- Frassinetti F, Fiori S, D'Angelo V, Magnani B, Guzzetta A, Brizzolara D, Cioni G. (2012). Body knowledge in brain-damaged children: a double-dissociation in self and other's body processing. *Neuropsychologia*. 50(1):181-8.
- Funk, M., Shiffrar, M., & Brugger, P. (2005). Hand movement observation by individuals born without hands: Phantom limb experience constrains visual limb perception. *Experimental Brain Research*, 164(3), 341-346.
- Gallagher, S. (2005). *How the body shapes the mind*. New York: Oxford University Press.

- Gallagher, S., & Meltzoff, A. N. (1996). The earliest sense of self and others: Merleau-Ponty and recent developmental studies. *Philosophical Psychology*, 9, 211-233
- Gallese V (2001) The 'Shared Manifold' hypothesis: from mirror neurons to empathy. *J Conscious Stud* 8(5-7):33-50
- Gallese V (2007) Embodied simulation: from mirror neuron systems to interpersonal relations. *Novartis Found Symp* 278:3-12
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, 119, 593-609.
- Gallese V, Sinigaglia C. (2011). What is so special about embodied simulation? *Trends Cogn Sci*. 15(11):512-9.
- Gazzola V, Rizzolatti G, Wicker B, Keysers C. (2007a). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *Neuroimage*. 35(4):1674-84.
- Gazzola, V., van der Worp, H., Mulder, T., Wicker, B., Rizzolatti, G., & Keysers, C. (2007b). Aphasics born without hands mirror the goal of hand actions with their feet. *Current Biology*, 17(14), 1235-1240.
- Georgieff, N. and Jeannerod, M. (1998) Beyond consciousness of external reality: a "who" system for consciousness of action and self-consciousness. *Conscious Cogn*. 7(3):465-77.
- Gillmeister H, Catmur C, Liepelt R, Brass M, Heyes C. (2008). Experience-based priming of body parts: a study of action imitation. *Brain Res*. 1217:157-70

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57
58
59
60
61
62
63
64
65
- Goldenberg G. (1995) Imitating gestures and manipulating a mannikin--the representation of the human body in ideomotor apraxia. *Neuropsychologia*. 33(1):63-72.
- Goldenberg G. (2009). Apraxia and the parietal lobes. *Neuropsychologia*. 47(6):1449-59
- Goldman, A.I. (2006). *Simulating minds*. Oxford: Oxford University Press
- Goldman, A.I. (2011) Two Routes to Empathy: Insights from Cognitive Neuroscience. In A. Coplan and P. Goldie (eds.), *Empathy: Philosophical and Psychological Perspectives*, pp. 31-44. Oxford University Press (2011).
- Goldman, A.I. (2012). A Moderate Approach to Embodied Cognitive Science. In A. Alsmith, & de F. de Vignemont (eds), *The body represented/Embodied representation*. *Review of Philosophy and Psychology*, Special issue, 3 (1).
- Goldman, A.I. and de Vignemont, F. (2009). Is social cognition embodied? *Trends in Cognitive Sciences*, 13(4), 154–9.
- Graziano, M.S.A. and Gross, C.G. (1993). A bimodal map of space: somatosensory receptive fields in the macaque putamen with corresponding visual receptive fields. *Exp Brain Res*, 97:96-109.
- Grezes J, Decety J (2001) Functional anatomy of execution, mental simulation, observation, and verb generation of actions: a meta-analysis. *Hum Brain Mapp* 12(1):1–19
- Guardia D, Conversy L, Jardri R, Lafargue G, Thomas P, Dodin V, Cottencin O, Luyat M. (2012). Imagining one's own and someone else's body actions: dissociation in anorexia nervosa. *PLoS One*. 7(8):e43241

- Hach S, Ishihara M, Keller PE, Schütz-Bosbach S. (2011). Hard and fast rules about the body: contributions of the action stream to judging body space. *Exp Brain Res.* 212(4):563-74.
- Haggard P. (2006). Just seeing you makes me feel better: interpersonal enhancement of touch. *Soc Neurosci.* 1(2):104-10.
- Head, H., and Holmes, G. (1911). Sensory disturbances from cerebral lesions. *Brain*, 34, 102–254.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends Cogn Sci.* 5(6):253-261.
- Iacoboni M, Molnar-Szakacs I, Gallese V, Buccino G, Mazziotta JC, Rizzolatti G (2005) Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol* 3(3):529–535
- Ishida H, Nakajima K, Inase M, Murata A. (2010). Shared mapping of own and others' bodies in visuotactile bimodal area of monkey parietal cortex. *J Cogn Neurosci.* 22(1):83-96.
- Jackson, P., Meltzoff, A. and Decety, J. (2005). How Do We Perceive the Pain of Others? A Window into the Neural Processes Involved in Empathy. *Neuroimage* 24:771–79.
- Jackson, P., Brunet, E., Meltzoff, A. and Decety, J. (2006). Empathy Examined through the Neural Mechanisms Involved in Imagining How I Feel versus How You Feel Pain. *Neuropsychologia* 44:752–61.
- Jeannerod, M. (1994) The representing brain: Neural correlates of motor intention and imagery. *Behavioral and Brain Sciences*, 17, 2, 187-202.

- Jeannerod, M. & Pacherie, E. (2004). Agency, Simulation and Self-identification. *Mind & Language*, 19, 2: 113-146
- Jungé, J.A and Dennett, D.C. (2010) Multi-use and constraints from original use. *Behavioral and Brain Sciences*, 33, 4.
- Kennett, S., Taylor-Clarke, M., Haggard, P. 2001. Noninformative vision improves the spatial resolution of touch in humans. *Curr Biol*. 11(15), 1188–91.
- Keysers, C., Wicker, B., Gazzola, V., Anton, J.L., Fogassi, L. and Gallese, V. (2004). A Touching Sight: SII/PV Activation during the Observation and Experience of Touch. *Neuron* 42:335–46.
- Keysers C, Kaas JH, Gazzola V. (2010) Somatosensation in social perception. *Nat Rev Neurosci*. 11(6):417-28.
- Makin, T.R., Holmes, N.P., Ehrsson, H.H. (2008). On the other hand: dummy hands and peripersonal space. *Behav Brain Res*. 191(1), 1–10.
- Meltzoff, A. N., & Moore, M. K. (1995). Infants' Understanding of People and Things: From Body Imitation to Folk Psychology. In J.L. Bermudez, A. Marcel, & N. Eilan (Eds.), *The Body and Self* (pp. 43-69), MIT Press: Bradford
- Myers A, Sowden PT. (2008). Your hand or mine? The extrastriate body area. *Neuroimage*. 42(4):1669-77.
- O'Shaughnessy, B. (1980). *The Will*. Cambridge: Cambridge University Press.
- Paillard, J. (1980). Le corps situé et le corps identifié. Une approche psychophysiologique de la notion de schéma corporel. *Revue Medicale de la Suisse Romande*, 100, 129–141.

- 1 Press C, Bird G, Flach R, Heyes C. (2005). Robotic movement elicits automatic
2 imitation. *Brain Res Cogn Brain Res*. 25(3):632-40.
3
4
5 Ramachandran VS, Brang D. (2009). Sensations evoked in patients with amputation
6 from watching an individual whose corresponding intact limb is being touched.
7
8 *Arch Neurol*. 66(10):1281-4.
9
10
11
12 Reed CL, Farah MJ (1995) The psychological reality of the body schema: a test with
13 normal participants. *J Exp Psychol Hum Percept Perform* 21:334–343
14
15
16 Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1995). Premotor cortex and the
17 recognition of motor actions. *Cognitive Brain Research*, 3, 131-141.
18
19
20
21
22
23
24 Rochat, P. (1998). Self perception and action in infancy. *Experimental Brain*
25
26 *Research*, 123, 102–109.
27
28
29 Rumiatì RI, Carmo JC, Corradi-Dell'Acqua C. (2009). Neuropsychological
30 perspectives on the mechanisms of imitation. *Philos Trans R Soc Lond B Biol*
31
32 *Sci*.364(1528):2337-47.
33
34
35
36
37 Schaefer M, Heinze HJ, Rotte M. (2012) Close to you: embodied simulation for
38 peripersonal space in primary somatosensory cortex. *PLoS One*. 7(8):e42308.
39
40
41
42 Schwoebel, J., and Coslett, H. B. (2005). Evidence for multiple, distinct
43 representations of the human body. *Journal of Cognitive Neuroscience*, 17,
44
45 543–553.
46
47
48
49
50 Shiffrar M, Freyd JJ (1990) Apparent motion of the human body. *Psychol Sci* 1:257–
51
52 264
53
54
55
56
57
58
59
60
61
62
63
64
65

- Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R. and Frith, C. (2004).
Empathy for Pain Involves the Affective but Not Sensory Components of Pain.
Science 303:1157–62.
- Spence, C., Pavani, F., Driver, J. (2004). Spatial constraints on visual-tactile cross-
modal distractor congruency effects. *Cogn Affect Behav Neurosci.* 4(2), 148–69.
- Thomas R, Press C, Haggard P. (2006). Shared representations in body perception.
Acta Psychol (Amst). 121(3):317-30.
- Tipper, S.P., Phillips, N., Dancer, C., Lloyd, D., Howard, L.A., McGlone, F. (2001).
Vision influences tactile perception at body sites that cannot be viewed directly.
Exp Brain Res. 139(2), 160–7.
- Tsakiris, M. (2010). My body in the brain: a neurocognitive model of body-
ownership. *Neuropsychologia.* 48(3), 703-12.
- Tsakiris, M., Haggard, P. (2005). The rubber hand illusion revisited: visuotactile
integration and self-attribution. *J Exp Psychol Hum Percept Perform.* 31(1), 80–
91
- Tsakiris, M., Prabhu, G., Haggard, P. (2006). Having a body versus moving your
body: How agency structures body-ownership. *Conscious Cogn.* 15(2):423-32.
- Wheaton KJ, Thompson JC, Syngeniotes A, Abbott DF, Puce A. (2004). Viewing the
motion of human body parts activates different regions of premotor, temporal,
and parietal cortex. *Neuroimage.* 22(1):277-88.
- Wood R, Gallese V, Cattaneo L. (2010). Visuotactile empathy within the primary
somatosensory cortex revealed by short-latency afferent inhibition. *Neurosci
Lett.* 473(1):28-31.

1 Zeller D, Gross C, Bartsch A, Johansen-Berg H, Classen J. (2011). Ventral premotor
2 cortex may be required for dynamic changes in the feeling of limb ownership: a
3
4
5 lesion study. J Neurosci. 31(13):4852-7.
6
7
8
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25 Action mirroring is considered as evidence of shared action representation, but can it
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